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ABSTRACT

The pygmy smelt, Osmerus spectrum Cope, 1870, is a valid lacustrine sibling species distinguished from the sympatric rainbow smelt, Osmerus mordax (Mitchill, 1815) by higher gill raker counts, relatively larger eye, lower lateral scale counts, and smaller maximum size. Transplant experiments demonstrate that gill raker and vertebral counts do not change significantly when smelt populations are transplanted to different environments. Spawning times of the pygmy smelt are later and do not overlap with those of the rainbow smelt when the two species are in the same lake.

The pygmy smelt is a planktivore throughout its life, while the rainbow smelt becomes piscivorous at larger sizes. The pygmy smelt grows more slowly, has a lower longevity, and spawns at a younger age. Pygmy smelt are identified from Heney Lake, Québec, Utopia Lake, New Brunswick, Green Lake and Wilton Pond in Maine. A topotypic neotype is designated from Wilton Pond and deposited in the National Museum of Natural Sciences, Ottawa.

Suggestions are made as to the time and place of origin of the pygmy smelt. Management implications of the existence of two species of smelts of different sizes are suggested. These include the value of pygmy smelt as a forage fish and the rainbow smelt as a gamefish.

RÉSUMÉ

L'éperlan nain, Osmerus spectrum Cope, 1870, est une espèce jumelle valable. On le distingue de l'éperlan arc-en-ciel sympatrique, Osmerus mordax (Mitchill, 1815) par un plus grand nombre de branchiospines, un nombre inférieur d'écailles de la ligne latérale, une plus petite longueur maximum et de plus gros yeux. Des expériences de transplantation ont démontré que le nombre de branchiospines et de vertèbres ne change pas de façon significative quand des populations d'éperlans sont transplantées dans des environnements différents. La fraie de l'éperlan nain a lieu plus tard et ne coïncide pas avec celle de l'éperlan arc-en-ciel quand les deux espèces se trouvent dans le même lac. L'éperlan nain est planctivore pendant toute sa vie, tandis que l'éperlan arc-en-ciel devient piscivore au stade avancé. L'éperlan nain croît plus lentement, atteint une plus petite longueur maximum et fraie à un plus jeune âge. On retrouve des populations d'éperlan nain au lac Heney, Québec, au lac Utopia, Nouveau-Brunswick, ainsi qu'au lac Vert et l'étang Wilton, Maine. Un néotype topotypique de l'étang Wilton est désigné; celui-ci est déposé au Musée national des Sciences naturelles, Ottawa.

On fait des suggestions relatives au temps et à l'endroit d'origine de l'éperlan nain. On mentionne aussi les implications pour l'exploitation de l'existence des deux espèces d'éperlan de différentes longueurs, y compris l'importance de l'éperlan nain comme poisson de pêche sportive.

ACKNOWLEDGEMENTS

Peter Cronin, New Brunswick Department of Natural Resources, Fredericton, provided data on and collected specimens of pygmy and rainbow smelt from Lake Utopia, New Brunswick. Michael J. Dadswell, Huntsman Marine Laboratory, St. Andrews, also collected specimens from Lake Utopia. Stanley W. Gorham, New Brunswick Museum, Saint John, established valuable contacts. L.N. Chao and the late James A. Böhlke sought the type specimens in museum collections. Vianney Legendre, then of the Service de la Faune, Montréal, coined the French vernacular name.

Brian W. Coad, Associate Curator, and Frederick Schueler, Research Associate, National Museum of National Sciences, Ottawa, criticized an early version and Claude Delisle, École Polytechnique, Université de Montréal, a later version of the manuscript. Schueler calculated the ANOVA of within and between-group variations for the pygmy smelt.

Jadwiga Anikowicz Frank made several radiographs. Aleta Karstad drew the pygmy smelt.

To all these persons the authors are grateful. Without their assistance the project could not have been completed.

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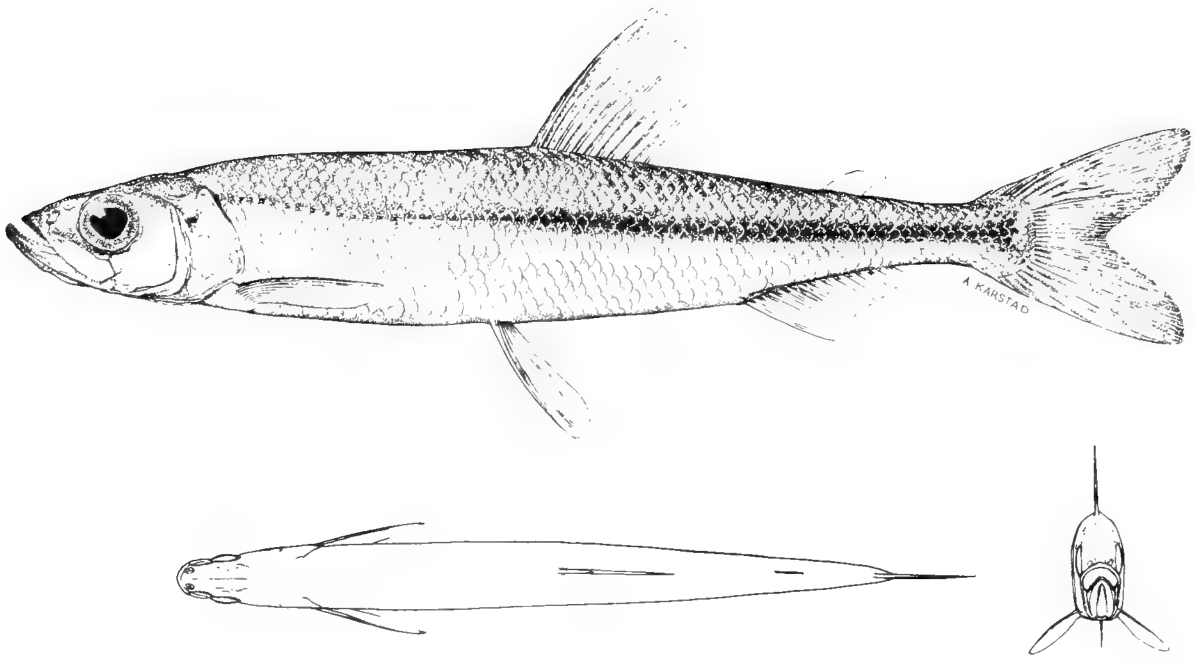

Fig. 1. Drawing of the neotype, NMC79-0834, of Osmerus spectrum Cope, 1870, a specimen 92.4 mm in standard length, collected in Wilton Pond, Franklin County, Maine, the type locality, on 29 August 1979. Drawing by Aleta Karstad.

INTRODUCTION

In 1870 Edward Drinker Cope, one of the deans of North American ichthyology, named a new species, Osmerus spectrum, from Wilton Pond, Franklin County, Maine, illustrated in Fig. 1. This species was treated by subsequent workers as a species, a subspecies, and later a full synonym of the rainbow smelt, Osmerus mordax (Mitchill, 1815). But recently, Delisle (1969a) and Copeman (1977) discovered morphologically separable sympatric populations, one large-sized, one small, in Lake Heney, Québec and Green Lake, Maine. Based on the solid foundations laid by these two workers and our own findings, we re-establish the smaller form as a valid species, for which the name Osmerus spectrum Cope, 1870 is available. This paper discusses the taxonomy of Osmerus spectrum, the stability of its characters when transplanted, its biology, distribution and origin. The management implications of the existence of two species of smelt are outlined.

Authors have discussed the two forms of smelts under a variety of common names, large smelt and small smelt, large and small races of smelt, dwarf and giant smelt, pygmy and normal smelt. To keep our discussions clear we will generally reserve the name pygmy smelt for populations that we identify as Osmerus spectrum Cope, 1870, and rainbow smelt for populations that we identify as Osmerus mordax (Mitchill, 1815). Where populations, which we have not examined and identified, differ in size, we will refer to them as small and large smelt.

HISTORY

Cope (1870) described Osmerus spectrum from two specimens collected in Wilton Pond near the head of the southwest branch of the Kennebec River in southwestern Maine. According to Kendall (1914) Wilton Pond is also known as Wilson Pond and is tributary to the Sandy River. Cope described a "medium-size" specimen as 3 in. 6 lin. (=3.5 inches = 89 mm, probably standard length). He further stated that "The characteristics of this species, according to Commissioner Atkins, are seen in specimens of larger size than those herein described, which were taken in breeding condition." Kendall (1927) later recorded specimens of breeding smelt 2-1/2 to 3-9/16 inches (57-80 mm SL) and one specimen 5-7/8 inches (about 133 mm SL) from Wilton Pond. Our own specimens from the Pond measure 72.6 to 100.8 mm in standard length (SL).

The type specimens of Osmerus spectrum apparently no longer exist. The late Dr. James A. Böhlke, (in lit., 17 July 1979) reported that he had checked the Philadelphia Academy of Natural Sciences type collection, general collection and type file without success. Nor did H.W. Fowler's (1912) list of salmonoids in the Academy contain reference to the smelt types. Dr. Böhlke further reported that many of Cope's types disintegrated or disappeared before reaching the Academy. Dr. Labbish N. Chao was unable to find the types in the Smithsonian Institute, Washington. It therefore appears that Cope's types of Osmerus spectrum are no longer in existence.

Cope (1870) followed the description of Osmerus spectrum, on the same page, with the description of another new species, Osmerus abbottii Cope, described from Cobessicontic

Lake, Kennebec County, southwest Maine (= Cobbosseecontee Lake which drains via Pleasant Pond into the Kennebec River). The identity of this species is less certain. Its size, 4 inches (= 102 mm probably SL), is closer to the size of the pygmy smelt than the rainbow smelt. Other features such as scale number suggest the rainbow smelt. The type specimens of *Osmerus abbottii* could not be located in the Academy of Natural Sciences by Dr. James A. Böhlke (*in lit.*).

Kendall (1914) listed 3 species of smelt for Maine: *Osmerus mordax*, *Osmerus spectrum* and *Osmerus abboti* (*sic*). Jordan and Evermann (1896) and Jordan, Evermann and Clark (1930) treated Cope's Wilton Pond smelt as a subspecies of *Osmerus mordax*. Hubbs (1925) in a revision of the family, recognized *Osmerus mordax* north of New York on the Atlantic coast and *O. sergeanti* Norris, 1868 south of New York. He omitted from his study *Osmerus spectrum* and *O. abbottii* which were being critically studied by W.C. Kendall (Kendall's taxonomic study was never published).

Kendall (1927) provided a valuable summary of the literature on the biology of eastern North American smelts and added much unpublished information of his own and others. He described the differing sizes of several populations but did not age specimens or report on other morphological differences.

Greene (1930) studied the smelts of Lake Champlain and commented that he could find no morphological differences between the large and small races. McAllister (1963), in his revision of the family, naively accepted Greene's verdict, and did not examine small smelt. He divided *Osmerus* into *Osmerus e. eperlanus* of Europe and *O. e. mordax* of the western Atlantic, Pacific and Arctic, according subspecific status at least until sympatric populations of the two forms were found not to interbreed. Klyukanov (1969) in his revision of the genus reported sympatric non-interbreeding populations in Arctic U.S.S.R., applied the name *O. eperlanus* to the European smelt, *O. m. mordax* to all eastern North American smelt, and distinguished Pacific and Arctic populations as *O. m. dentex*; he did not discuss *O. spectrum*.

Zillox and Youngs (1958) studied the smelt in Lake Champlain and divided them into a large race and a small race. A winter specimen of each shown in a photo were 233 mm and 158 mm TL. The angler's catch averaged 84% of the large and 16% of the small smelt. Comparisons of growth of large smelt in 1929 and 1950 showed little substantial change; of 10 age samples compared, only two differed significantly. Thus growth within a "race" in this lake appears relatively constant.

Rupp and Redmond (1966) summarized the results of valuable experimental transplants of six established smelt populations into eight new lake environments. They reported changes in growth rate and longevity between source and transplanted stocks. They found that "little" smelts became "big" smelts when transplanted to a reclaimed (rotenoned) lake and concluded the effect of genotype was small in comparison with the potential influence of the environment; thus implying that big and little smelt populations were largely environmental in origin. The early spawning habit did appear to be under genetic control, however.

Copeman and McAllister (1978) re-analyzed the data of Rupp and Redmond (1966) plus some more recent data on these transplanted populations. Copeman and McAllister (1978)

TABLE 1. *Source and size of smelt samples studied.*

Species Locality	N	NMC Catalogue Number	Date of Capture/ Collector	Standard Lengths Minimum - Maximum (in mm)
P Heney Lake, Gatineau Co., Quebec	18	67-809	March 1965 C. Delisle	70.1 - 79.6
P Same	3	68-167	4 June 1968 W.H. Van Vliet	76.8 - 94.5
R Same	3	68-167	Same	100.9 - 111.2
P Same	3	76-151	12 Sept. 1971 P.J. Pubec	72.6 - 76.7
R Same	4	76-151	Same	130 - 141
P Same	2	68-151	10 May 1968 W.H. Van Vliet	72.6 - 76.7
R Same	2	68-151	Same	163 - 184
P Utopia Lake, Charlotte Co., New Brunswick	32	80-505	12 May 1980 B. Bradford	81.2 - 113.7
P Same	18	80-507	9-10 May 1980 J. Berry	82.7 - 111.3
R Same	21	81-1110	7 April 1981 N.B. Dept. Nat. Res.	141.8 - 205.1
P Wilton Pond, Franklin Co., Maine	19	79-835	29 Aug 1979 Arsenault & Farrell	72.6 - 100.8
NEOTYPE:				
P Same	1	79-834	Same	92.4

(P = pygmy smelt, R = rainbow smelt, N = sample size, NMC = National Museums of Canada)

interpreted the data as showing that smelts may show an initially accelerated or prolonged growth when introduced into a reclaimed lake, but that later the growth characteristics of the transferred population return to those of the source populations. Meristic characters were little affected by the transfer. Copeman and McAllister (1978) concluded that extended analysis of the transplant data did not refute the hypothesis that there are two hereditarily different forms of smelt. The existence of reproductively isolated populations of large and small smelt is not easily explained by the environmental hypothesis. Gill raker counts suggest that the populations transferred were pygmy smelts.

Delisle (1969a) and Legault and Delisle (1968) studied growth, life history, ecology and taxonomy of smelt in Lake Heney, Gatineau County, Québec. This lake is 143 m above sea level and drains into the Gatineau River, a tributary of the Ottawa River. Delisle (1969a) found the pygmy smelt population averaging 120 mm at 5 years and the sympatric population of rainbow smelt exhibiting more rapid growth and averaging 230 mm total length (TL) at the same age. The rainbow smelt spawned at 4 degrees C before ice break-up, March 17 to April 12; the pygmy smelt at 4-8 degrees C, between April 2 and May 10, after break-up. At larger sizes the rainbow smelt fed at a higher trophic level and preyed upon the pygmy smelt, while the pygmy smelt was planktivorous throughout life. Delisle (1969a) also found differences in meristic and morphometric characters some of which permitted 100% separation of the two populations. Delisle (1969a) concluded that additional studies were needed before the two populations could be distinguished as species.

Bridges and Delisle (1974) studied visual pigments in pygmy smelt, and in anadromous and lacustrine rainbow smelt. They found that pygmy smelt in Lake Utopia (in May), New Brunswick had 92% rhodopsin and had 93-97% rhodopsin when transplanted to Meach Lake (May) and Lake Ouimet (May-June), Quebec. Pygmy and rainbow smelt from Lake Heney (March-October) had only 0-4%, while St. Lawrence River samples varied from 96.2% (in spring) to 9.3% (in summer). The results are difficult to explain, but suggest at least one possible difference between pygmy smelt from lakes Utopia and Heney and the existence of annual changes within populations.

Copeman (1973, 1977) performed multivariate analyses of 32 mensural and meristic characters on 12 spawning site samples of anadromous and lacustrine smelts from eastern North America. Pygmy smelt from Green Lake (tributary of Union River), Hancock County, Maine and Lake Heney, Québec, were morphologically 100% separable from both lacustrine and anadromous rainbow smelts using all characteristics, 92.5% and 97.5% separable using total gill rakers alone, and all meristic characters respectively. He did not study directly the rainbow smelt reported from Green Lake, Maine, but did study smelt in lakes Superior, Huron and Erie descended from a 1912 planting of rainbow smelt from Green Lake into Crystal Lake, Michigan. Between anadromous and lacustrine rainbow smelts groups 99.0% correct identification was achieved using all characters, 89.1% with total gill rakers and 91.3% using both gill rakers and vertebrae. He indicated that identification success and biological data fulfilled criteria for species recognition of the pygmy smelt, and that identification levels for anadromous and lacustrine rainbow smelt suggested subspecific status. He felt that before formal species recognition was accorded the pygmy smelt, that

TABLE 2. *Statistics for pygmy and rainbow smelt samples. (Mean ± one standard deviation, range)*

Species Population	Sample Size	Standard Length (mm)	Orbit Diam/%SL	Caudal Ped. Depth/%SL	Number gill rakers	Number mid-lat. scales	Number Vertebrae
O. spectrum (neotype)	1	92.4	6.0	6.3	35	63	62
O. spectrum	19	88.90±8.31	5.33±0.43	6.1±0.31	33.89±0.94	62.68±0.75	62.03±0.67
Wilton Pond, Maine		72.6-100.8	4.4-6.1	5.2-6.7	32-36	62-64	61-63
Utopia Lake	50	96.89±10.62	5.5±0.56	6.27±0.36	34.12±0.77	61.04±1.16	61.72±0.73
New Brunswick		81.2-113.7	4.5-6.5	5.5-6.9	33-36	59-63	60-63
Heney Lake	24	76.90±4.31	5.27±0.39	6.33±0.53	34.29±0.95	61.21±1.59	60.42±0.72
Quebec		70.1-94.5	4.6-6.2	5.2-7.5	32-36	58-65	59-62
Osmerus mordax							
Utopia Lake	21	177.89±18.56	9.36±0.87	6.25±0.25	31.05±1.40	64.43±0.81	62.09±0.44
New Brunswick		141.8-205.1	7.9-11.3	5.7-6.8	28-33	63-66	61-63
Heney Lake	10	138-71±29.48	8.56±1.20	6.01-0.26	31.69±1.43	62.80±1.87	61.10+0.74
Quebec		100.9-184.0	7.0-10.4	5.7-6.4	29-34	61.67	60-62
Combined sample							
O. spectrum	93	90.10±12.21	5.4±0.50	6.25±0.41	34.12±0.87	61.42±1.37	61.44±0.94
		70.1-113.7	4.4-6.5	5.2-7.5	32-36	58-65	59-63
Combined sample							
O. mordax	31	165.25±28.93	9.10±1.04	6.17±0.28	31.23±1.41	63.90±1.45	61.77±0.72
		100.9-205.1	7.0-11.3	5.7-6.8	28-34	61-67	60-63

it was desirable to examine other lakes, especially for pygmy smelt, to see whether they fell reasonably well into one of the categories. We try to accomplish this and other goals in the present paper.

Luey, Krueger and Schreiner (1982) examined proteins of Osmerus samples using electrophoretic methods. Samples from Lake Huron (originating from rainbow smelt in Green Lake, Maine) were closer to a sample of the western European smelt from Lake Ijssel, Netherlands, than to Osmerus mordax dentex from Alaska. The genetic distances suggested that the Alaskan samples were specifically distinct from the two Atlantic basin collections which were closer than would be expected for congeneric species. This contrasts with Klyukanov's (1975) results; he found 7 osteological and meristic characters which linked O. m. mordax to O. m. dentex, but only 2 which linked O. m. mordax to O. eperlanus.

MATERIALS

One hundred and twenty-six specimens of both types taken from three geographical areas were examined (Table 1). The samples from Lake Utopia were taken during the populations' spawning runs and were composed of sexually mature individuals. All samples were fixed in 10% formalin and preserved in 50% isopropyl alcohol. An additional sample of 14 pygmy smelts from Meach Lake, Gatineau Park, Québec, which originated from a transfer from Utopia Lake, New Brunswick, were examined in the final stages of this study, but not included in all the analyses.

METHODS

Counting and Measuring

Body measurements were made with Helios dial calipers to the nearest 0.1 mm, according to the methods of Legendre (1952). Vertebral counts, including the urostyle, were made from X-rays taken on a Softex EMB machine using Kodak Type M2 film. Gill raker counts, including the rudiments, were made under a binocular microscope. Scale counts were made along the midlateral line to the caudal flexure.

Statistical Methods

The principal components analysis (PCA) program of Davies (1971) was translated from FORTRAN to BASIC and run using a Hewlett-Packard 9845 minicomputer with 12 digit precision. Measurements were converted to log to the base 10. The meristic values and log measurements were standardized by subtracting the mean value for that character and dividing by the standard deviation of that character. The PCAs were run using these values in correlation matrices.

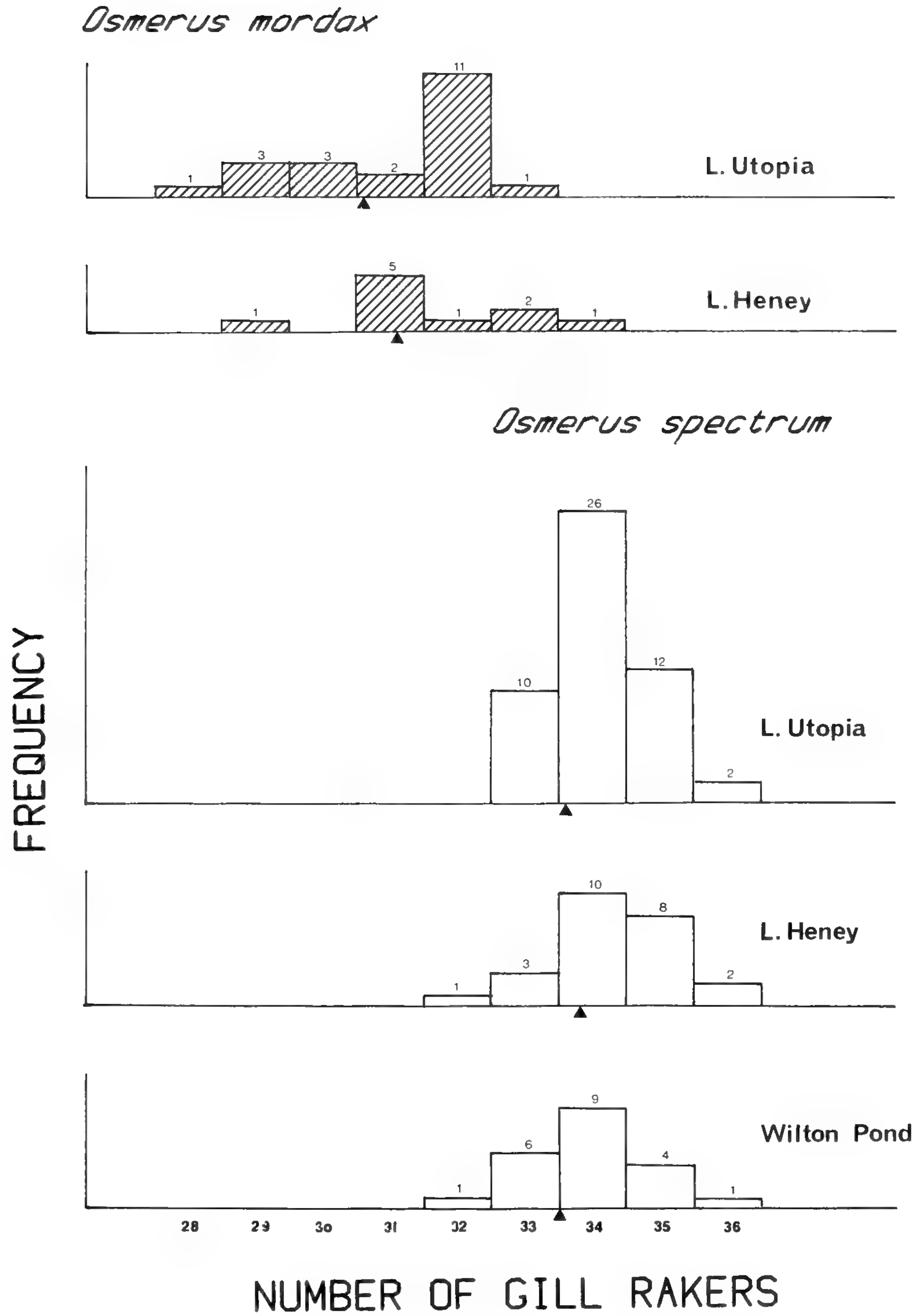

Fig. 2. Frequency of gill raker counts in population samples of pygmy smelt, Osmerus spectrum and rainbow smelt, Osmerus mordax.

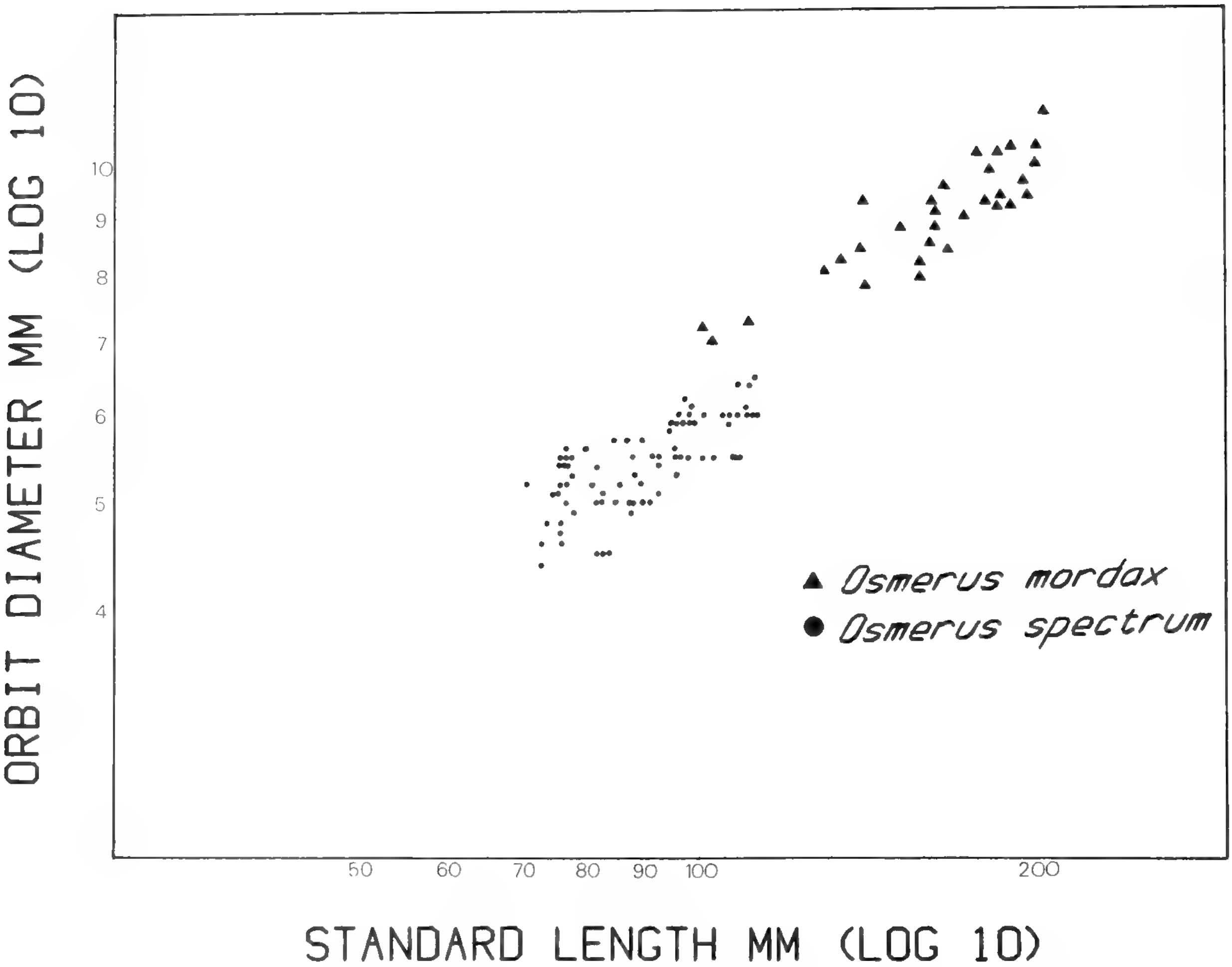

Fig. 3. Relative growth differences in orbit diameter and standard length on a logarithmic scale, in pygmy smelt, Osmerus spectrum and rainbow smelt, Osmerus mordax.

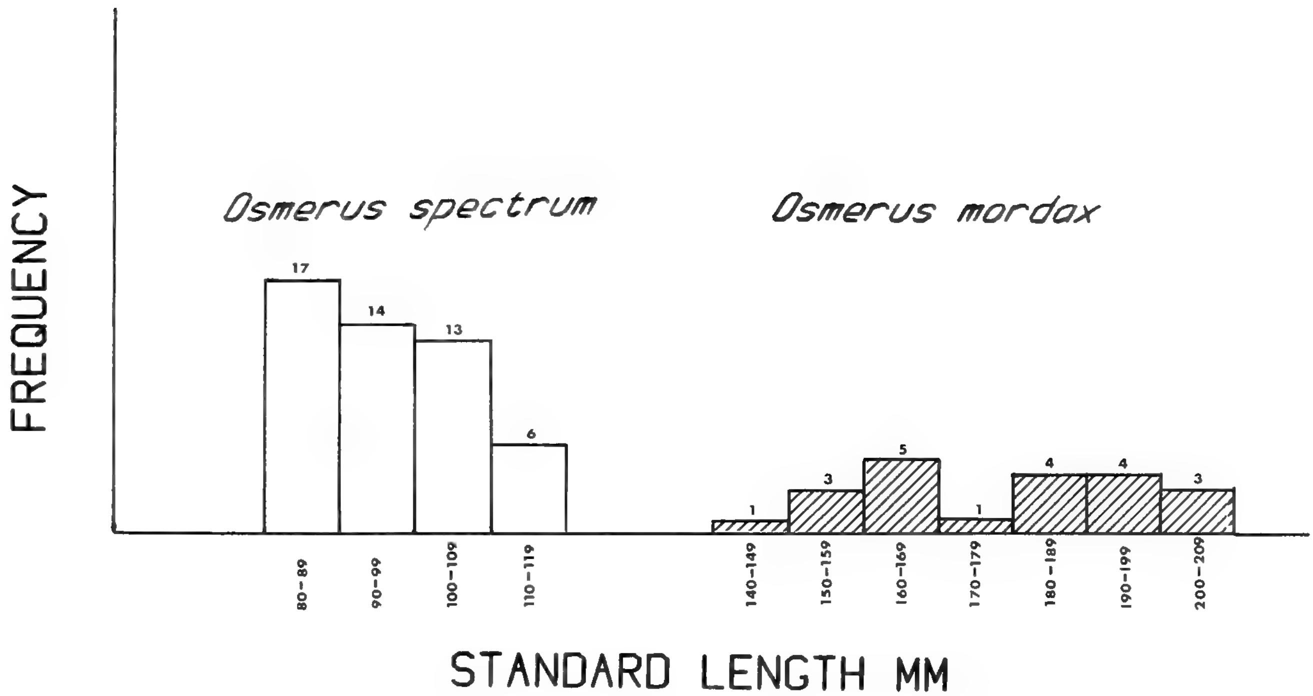

Fig. 4. Frequency of standard lengths in 50 pygmy smelt, Osmerus spectrum and 21 rainbow smelt, Osmerus mordax, from Utopia Lake tributaries captured May 9, 10 and 12, 1980.

MORPHOLOGICAL RESULTS

The sources, samples sizes, body lengths and other details on smelt samples studied are presented in Table 1. Ranges, means and standard deviations of characters are given for each population of smelt studied in Table 2. Frequency of gill rakers in each population is shown in Fig. 2 and relationship of orbit diameter to standard length in Fig. 3. Fig. 4 shows the length frequencies of the spawning pygmy and rainbow smelt samples in Utopia Lake, New Brunswick; other samples, not taken at spawning time, are not shown.

Principal components one and two are plotted in Fig. 5 and show complete separation of pygmy and rainbow smelts. Latent vectors are shown in Table 3. Latent vectors one and two subsumed 83% of the variance. Principal components 3 to 6 did not aid in separating the pygmy and rainbow smelts. PCA runs with data unlogged but standardized, and with raw data gave substantially similar results in separating the pygmy and rainbow smelts.

BIOLOGICAL DATA

Reproduction

In Lake Heney, Québec, rainbow smelt spawn before ice break-up in water about 6 m deep and below 4 degrees C, from March 17 to April 12. The pygmy smelt spawn following break-up at an average temperature of 6 degrees C on sand and gravel beaches between April 22 and May 10 (Delisle, 1969a).

In Green Lake, Maine, rainbow smelt were caught from March 25 to April 20, while pygmy smelt were caught from May 5 to May 20 according to Kendall (1927, p. 296). Copeman (1973) reported there was a period of at least 8 to 16 days between spawning runs of the rainbow and pygmy smelts where spawning did not occur. In Utopia Lake, New Brunswick, our collections of spawning rainbow smelt were taken in Mill Stream at the northeast end of the lake on 7 April 1980 at 4 degrees C, while pygmy smelt were collected in Mill Brook on the northwest shore 12 May 1981. Pygmy smelt spawn in Mill Stream, at the northeastern end of the lake, in 15 to 60 cm of water; a dam between Lake Utopia and Mill Lake prevents the smelt from entering Mill Lake (Peter Cronin, pers. comm.). Bridges and Delisle (1974) reported pygmy smelt spawning in Lake Utopia 22 May 1972. A population of pygmy smelt transplanted from Utopia Lake to Meach Lake, Gatineau County, Québec (Dymond, 1939; Delisle and Veilleux, 1969) was spawning on 8 May 1963 (collection NMC71-651), and 19 May 1971 (Bridges and Delisle, 1974). Although the large and small smelt of Sebago Lake, Cumberland County, Maine has not been (yet) shown to correspond to rainbow and pygmy smelts, Kendall (1927) nevertheless reported that the large smelt ran before the small smelt, and often as soon as the ice is out and sometimes before, a sequence which corresponds to the above pattern.

While over the whole range of the two smelt species there may be an overlap in spawning times, there seems to be a separation in their spawning periods when the two are found in the same lake, and the pygmy species spawns later than the rainbow smelt. There may be a balance struck between selection for the faster development in warmer water, the lower

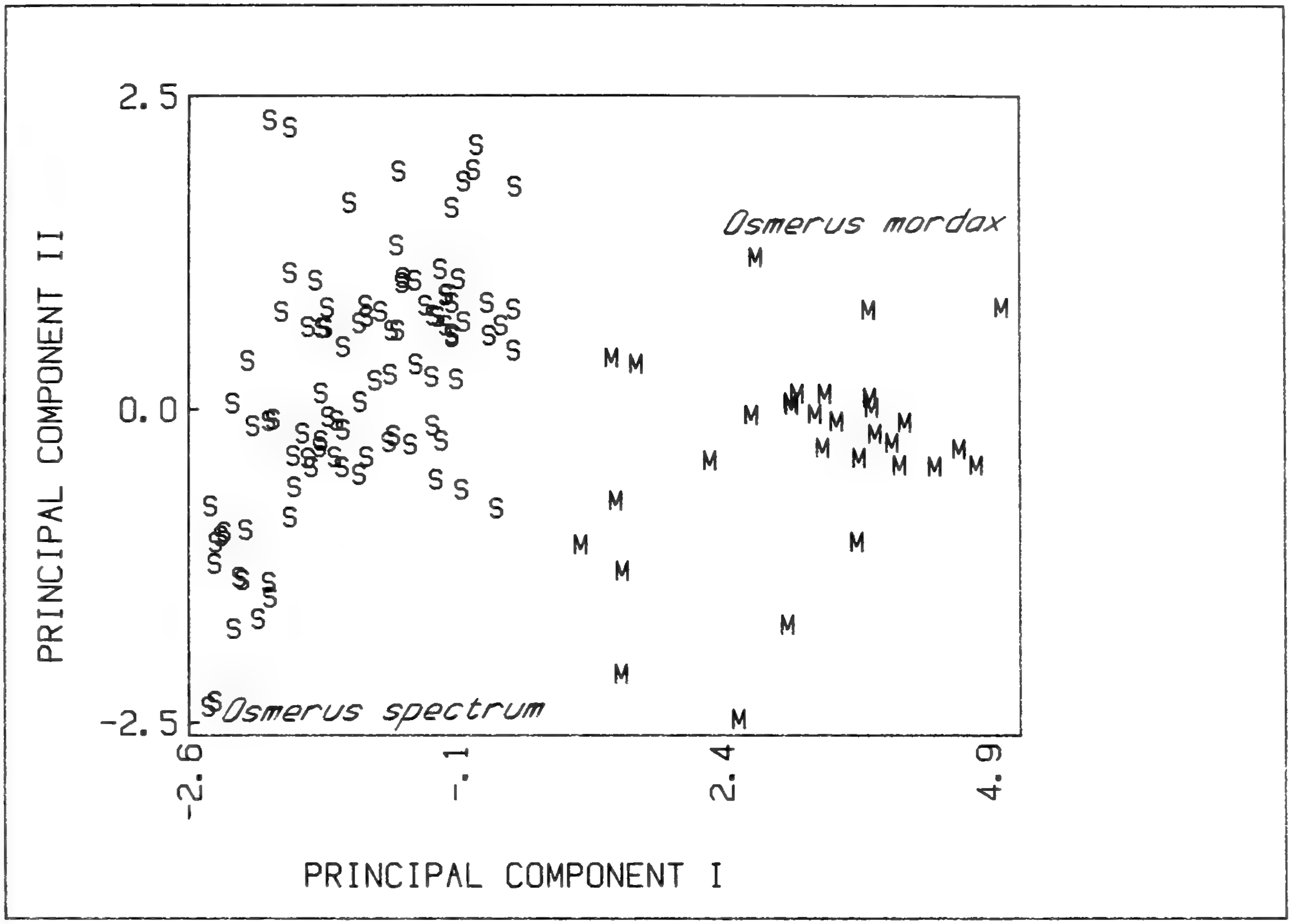

Fig. 5. Principal components analysis of pygmy smelt, Osmerus spectrum (S) and rainbow smelt, Osmerus mordax (M) from Wilton Pond, Maine, Utopia Lake, New Brunswick and Heney Lake, Québec with standardized data.

TABLE 3. *Latent Roots, Latent Vectors, and % Variances of Principal Components Analysis*

Component	1	2	3	4	5	6
Latent Roots						
	4.034	0.934	0.570	0.387	0.057	0.018
Percent Variance						
	67.2%	15.6%	9.5%	6.4%	0.96%	0.31%
Latent Vectors						
Character						
Standard Length	0.480	-0.077	0.264	0.153	-0.303	-0.761
Orbit Diameter	0.466	-0.240	0.193	0.179	0.804	0.101
Caudal Peduncle depth	0.474	-0.110	0.305	0.137	-0.492	0.640
Gill Rakers	-0.396	0.192	0.334	0.833	0.212	0.006
Scales Midlateral	0.357	0.250	-0.789	0.429	-0.042	0.029
Vertebral Centra	0.207	0.908	0.257	-0.217	0.134	0.031

predation under ice, and against the gamete wastage through hybridization resulting from overlapping spawing times.

According to Delisle (1969a) ovarian eggs ranged from 0.80 to 0.95 mm in the rainbow smelt but only 0.54 to 0.65 mm in the pygmy smelt.

Food

Delisle (1969a) found that the rainbow smelt tended to feed at a higher trophic level; over 50% of its diet in Lake Heney consisted of adult pygmy and young pygmy and rainbow smelts. They also ate invertebrates such as *Mysis*, copepods and Ephemeroptera. The food of the pygmy smelt on the other hand, was composed largely of plankton, mainly adults and eggs of *Daphnia*, and adult *Cyclops* and *Bosmina*.

Kendall (1927) reported that small smelt (3-1/32 to 3-7/8 inches = 77-98 mm) dynamited in Wilton Pond in spring contained gnat and caddis fly larvae and small Diptera. In Sebago Lake he found that large smelt were piscivorous (most commonly on smelt). In Lake Utopia, New Brunswick, Bajkov (MS 1936) found pygmy smelt to be planktivorous, feeding mostly on *Diaptomus*, *Cyclops*, *Leptodora*, *Daphnia*, *Epischura*, and *Bosmina*. He found rainbow smelt in the lake fed mostly on small smelt. Rainbow smelt were occasionally caught on artificial flys at the surface.

Size, Age and Growth

The maximum total length of pygmy smelt in Lake Heney is less than 125 mm TL, that of rainbow smelt about 300 mm (Delisle, 1969a). Delisle noted that the pygmy grows more slowly, at five years reaching only 120 mm TL and 74 g. The maximum age he gave for the pygmy smelt was 5 years, but only 11% reached 4 years of age and 2%, 5 years; for rainbow smelt the maximum was 6 years with 31% reaching 4 years and 4%, 6 years. The pygmies reached sexual maturity at 2 years while most of the rainbows required 3 years. Copeman (1977) found his spawning samples of pygmy smelt from Heney and Green lakes to consist entirely of 2 year-olds (mean standard length 75.8 mm), while Heney rainbow smelts consisted of 25% 3 year-olds, 65% 4 year-olds, and 10% 5 year-olds ranging from 157-206 mm SL. The large and small smelts in Lake Champlain have not yet been proven identical to the rainbow and pygmy smelts; nevertheless Greene (1930) found in winter angling catches that the small form was composed of 1 to 3 year-olds with mean lengths 121-130 mm SL, and the large form of young-of-the-year to 5 year-olds 131 to 249 mm SL. The small form matured in their second year while only 31% of the two-year-old large smelt were mature.

These admittedly limited data suggest that, at least when sympatric, pygmy smelt grow more slowly, mature earlier, and have a shorter life span. The results of Copeman and McAllister (1978), Zillox and Youngs (1958), and the Green Lake transplant to the Great Lakes, suggest that under natural conditions, growth rates of a given species are relatively constant within a lake.

Habitat

All of the lakes in which the presence of pygmy smelt has been verified, are small, deep and thermally stratified in summer. Lake Heney is an oligotrophic lake about 9 km long, 1250 hectares, has an average depth of about 18 m and a maximum depth of 35 m. In June the thermocline extends from about 2 to 3 m. The Secchi disk reading varies from about 3 to 6 m. The mean pH in Heney Lake in 1966-67 was 7.3. The lake freezes over from 8-28 December and break-up occurs from 23 April to 1 May (all preceding details from Delisle, 1969a). Wilton Pond, Maine is approximately 4 km long, Green Lake, Maine about 9 km, and Lake Utopia, New Brunswick about 8 km long. So all lakes in which pygmy smelt are definitely known are small, 9 km or less in length.

The following details on Lake Utopia are drawn from data in the files of the Fish and Wildlife Branch, New Brunswick Department of Natural Resources, through the courtesy of Mr. Peter Cronin. The surface area is 1370 hectares, the mean depth 11.05 m, the maximum depth 25.6 m, the morpho-edaphic index 0.94, the pH 7 at the surface, 6.7 at 11 m, and 6.4 at 26 m. On 27 August 1969 the thermocline was located between 10 and 15 m depth, and on 3 July 1969 the surface temperature was 19 and the bottom at 25 m was 7.8 degrees C.

Rainbow smelt are known in lakes large and small, although most are probably deep and thermally stratified in summer. Lake Champlain which might contain both species is about 130 km in length. Lake Superior into which rainbow smelt have been successfully introduced, is more than 500 km long. Many rainbow smelt populations are anadromous and live in the sea after hatching until as adults they run up streams and rivers to spawn in spring.

The following additional notes on habitat and movement are drawn from Delisle's (1969a) valuable thesis. Young-of-the-year pygmy smelt, but not rainbow smelt, aggregate in shallow water near sand and gravel beaches in July, August and winter. In July pygmy smelt adults migrate up into the epilimnion (21 degrees C) from the bottom in the hypolimnion (7-9 degrees C), at 2300 to 0200 hours. The adult pygmy smelt was found to form schools beneath the ice in January.

Before spawning in April, pygmy smelts migrate from the depths to the surface between 0100 and 0400 hours. The rainbow smelt was found throughout the year in the deeper southern basin of the lake, except at spawning time, and was not observed to make vertical migrations or be attracted to lamps at night.

The evidence suggests that there are habitat and behavioral differences between pygmy and rainbow smelts. That separation is not complete, however, is attested by the presence of pygmy smelts in the stomachs of rainbow smelts.

TRANSPLANTATION EXPERIMENTS

Transfer of species from one lake to another lake with differing conditions may assist in determining if taxonomic characters have a genetic base.

In 1912 rainbow smelt from Green Lake, Maine, were transplanted into Crystal Lake, Michigan. From there the smelt spread into each of the Great Lakes. Despite marked temperature and productivity differences between lakes Superior and Erie, populations from

these two lakes clustered together in canonical analyses (Fig. 1, Copeman, 1977) in closer proximity to other rainbow smelts from Lake Huron and Lake Heney. Divergence of introduced populations after more than 60 years was equivalent to that between other natural populations. But the changes resulting from direct environmental differences during development and from selection was not such as to cluster any population with the pygmy smelt.

Similarly Copeman and McAllister (1978) interpreted the results of smelt transfer experiments in Maine to show that, although growth may be initially accelerated or prolonged in a population transplanted into a previously rotenoned lake, that in a second phase these effects subside and growth characteristics return to those of the source populations. Copeman and McAllister (1978) found that gill raker and vertebral counts were not significantly changed between source and host lakes in the initial or secondary phases of transfer experiments.

Pygmy smelt from Utopia Lake, New Brunswick, were transplanted to Meach Lake, Gatineau County, Québec about 1924 (Dymond, 1939). A collection of 14 specimens made in Meach Lake on 8 May 1963 (NMC71-0651) was located just before the present manuscript was completed. Chi-square tests showed that neither gill raker nor vertebral counts were significantly different (p more than 0.30) in samples from the two lakes, despite climatic differences and the passage of nearly 40 years. It may be noted that gill rakers were shown in Copeman's (1977) and the present study to be the best meristic diagnostic character.

DISCUSSION

Taxonomy

In this discussion we shall attempt to answer whether the pygmy smelt is a species distinct from the rainbow smelt and what scientific name should be applied to the pygmy smelt. Species are understood here to consist of a population or populations of actually or potentially interbreeding organisms which are reproductively isolated from other such groups and are usually morphologically distinct.

Morphological evidence from Delisle (1969a), Copeman (1973, 1977), and the present study indicate that pygmy and rainbow smelts are morphologically distinguishable. Transplantation experiments cited demonstrate that the number of gill rakers and vertebrae have a genetic basis and are little affected by transplantation to environments very different in temperature, productivity and other factors. Growth under equilibrium conditions of lakes (second phase in reclamations), appears to exhibit an underlying genetic basis.

In Heney, Green and Utopia lakes evidence has been cited that pygmy and rainbow smelts spawn at different times and that the spawning periods do not overlap in sympatric populations. Rupp and Redmond's (1966) data on transplants in Maine indicate that spawning time is under genetic control and is not significantly influenced by transfer to another lake. A transplanted population in Meach Lake, Québec, spawned at essentially the same time (8-19 May) as the source population in Utopia Lake, New Brunswick (12-22 May).

It might be argued that pygmy smelt arose independently through parallel evolution in the four lakes where it is known. For the characters to have evolved in the same direction by chance in the four lakes is quite improbable. The results of the multivariate analyses by Copeman (1977) and the present study make it extremely unlikely that the pygmy smelt populations arose independently, in spite of the non-concordance of one character, the visual pigment. Additionally an hypothesis of independent origin of each pygmy smelt population would have to cope with similarities in spawning times of at least three pygmy smelt populations, with slower growth rates and the earlier maturity of the two pygmy smelt populations studied. These data cause no problem for the common origin hypothesis. We therefore reject the hypothesis of independent origin of each pygmy smelt population.

The lacustrine non-migratory pygmy smelt may suggest similarity to the kokanee, a lacustrine non-migratory form of the anadromous sockeye salmon, Oncorhynchus nerka. However, Nelson (1968a) found geographic and geological evidence that at least some of the populations of kokanee had independent origins through the development of falls, or the blockage of rivers by lava or glaciers. And Nelson (1968b) showed that some kokanee had higher gill raker counts than sympatric sockeye salmon (Stewart and Anderson lakes), while the Takla Lake the kokanee had fewer gill rakers than the sockeye. Although gill raker counts were significantly different between sympatric kokanee and sockeye, none permitted even subspecific levels of separation. Additionally, Nelson (1968b) found the range of means of gill rakers in 8 allopatric kokanee populations and 11 kokanee populations sympatric with sockeye, encompassed the range of means known for sockeye populations. We concur with Nelson (1968a) that it is highly likely that kokanee had multiple origins and that both forms should be designated as Oncorhynchus nerka.

We bring the kokanee example forward to contrast the example of a form with a multiple origin with the condition in the pygmy smelt where gill raker counts, body size and growth, and spawning times all differ in a consistent pattern from sympatric rainbow smelt. Further we have shown that gill raker counts permit high levels of separation (90%) of the pygmy and rainbow smelts, whether sympatric or allopatric. All specimens of pygmy and rainbow smelts can be distinguished using multivariate analysis. Pygmy and rainbow smelt are reproductively isolated.

There is one race of a dwarf (not the pygmy smelt) smelt in eastern North America that probably did have an independent origin. In Black River Pond, Avalon Peninsula, Newfoundland, there is a dwarf form of smelt with mean size of two-year-olds of 98 mm fork length and a sympatric large smelt averaging 152 mm at the same age. Interestingly, here the small and large smelt did not differ significantly in gill raker number which was maximally 32, and the dwarf feeds mainly on benthic insects. There is an overlap of one day in their spawning times. The preceding information was drawn from Bruce MS (1975). Insular Newfoundland was apparently completely glaciated. If the lacustrine dwarf evolved in insular Newfoundland, which seems possible, then it can be no older than 15,000 years BP. It seems likely from deglaciation and gill raker evidence and the depauperate freshwater fauna of the island that the Newfoundland dwarf evolved separately from the mainland pygmy smelt. Mann and McCart (1981) found that the dwarf cisco, Coregonus sardinella, had

significantly fewer gill rakers than a sympatric population of normal size in Trout Lake, Yukon Territory. These examples demonstrate that dwarfing need not be accomplished by planktivory or by gill raker increase.

We conclude that the morphological, ecological and reproductive data indicate that the pygmy smelt is a distinct species from the rainbow smelt.

We consider the pygmy smelt as a sibling species because no single character distinguishes it from the rainbow smelt and multivariate analysis is needed to identify all non-spawners. In the usage of Rising and Schueler (1980) it might therefore be called a morphological sibling species. However, those authors suggest calling siblings those species having more within-group variation than between-group variation. But in our case, the among-group variation, as measured by a one way ANOVA of the first principal component, was 91.6% and exceeded the within-group variation, 8.4%. However, these percentages might be expected to change if populations of pygmy smelt are analyzed and when anadromous rainbow smelt samples are added.

Nomenclature

Copeman (1977) has shown that anadromous and lacustrine rainbow smelt are distinguished from one another at a level approximately characteristic of subspecies. For the present, because lacustrine rainbow smelt, occurring in Newfoundland and on the mainland, do not have a continuous distribution required of a subspecies (Bailey, Winn and Smith, 1954), lacustrine and anadromous rainbow smelt will be treated for the moment as a monotypic species. The name *Osmerus mordax* (Mitchill, 1815) is the earliest name available for this form; Klyukanov (1969) refers the eastern North American smelt to *O. m. mordax* (Mitchill, 1815), distinguishing it from *O. m. dentex* Steindachner, 1870 of the Pacific and Arctic oceans and drainages.

Concerning the pygmy smelt, only two lacustrine populations of smelt have been named in eastern North America, *O. spectrum* in Wilton Pond, Maine and *O. abbottii* in Cobessicontic Lake, Maine, both by Cope (1870). The type specimens of both are missing, as noted earlier. Topotypic material of *Osmerus abbottii* is not available to us and Cope's original description does not permit us to determine which of the two species of smelts he had in hand.

Topotypic material of *Osmerus spectrum* and the small size of Cope's specimens (89 mm SL), said to be breeding, suggest that he most likely had the pygmy smelt in hand. But Cope's description when compared with that of Delisle (1969a) leave some doubt as to the identity of Cope's specimens. While the length of the head, 4.25 times in length, eye one third of head length, and the 10 anal fin rays favour identification with the pygmy smelt, the high number of lateral line scales is characteristic of the rainbow smelt. It is possible that both pygmy and rainbow smelt are found in the lake. Cope did mention that larger specimens were known and exhibited the characteristic features of the species. Kendall (1927) reported a specimen 5-7/8 inches (133 mm SL) long. Because there are some legitimate doubts as to the identity of Cope's types and because his type specimens are missing, it appears desirable to fix the identity of Cope's name. We therefore designate NMC79-0834, a specimen

92.4 mm in SL, collected by gill net at 15 m in Wilton Pond, Maine, on 29 August 1979 by K. Farrell as the neotype of Osmerus spectrum Cope, 1870; the neotype was collected at the type locality of the species. The neotype is illustrated in Fig. 1. The neotype has the following characters additional to those in Table 1: body depth 15.5 mm, head length 21.4 mm, primary dorsal rays 10, primary anal fin rays 15, pelvic fin rays 8, pectoral fin rays 12, pored lateral line scales 16, longest gill raker 2/3 of orbit diameter, pelvic origin slightly in advance of dorsal origin, maxillary ends just before hind edge of pupil, lower jaw projects beyond upper, gonads undeveloped.

Osmerus spectrum Cope, 1870 has been referred to by a number of names in the vernacular: Wilton Pond smelt, small smelt, small race of smelt, and dwarf smelt. Because we feel that none of these are appropriate, we coin the name pygmy smelt as its English vernacular, and Vianney Legendre has suggested éperlan nain as its French vernacular.

Key to lacustrine Osmerus in eastern North America

1 (2) Standard length less than 135 mm. Gill rakers usually 33-36. Orbit diameter 4.4-6.5% of standard length . . . . pygmy smelt - Osmerus spectrum Cope, 1870

2 (1) Standard length up to at least 200 mm. Gill rakers usually 28-32. Orbit diameter 7.0-11.3% of standard length . . . . rainbow smelt - Osmerus mordax (Mitchill, 1815)

Distribution

We have established that Osmerus spectrum is native to Heney Lake, southern Québec, Lake Utopia, southern New Brunswick, to Wilton Pond and Green Lake, southern Maine, and has been transplanted to Meach and Ouimet lakes, Québec (Figure 6). Its existence elsewhere is suggested by literature reports.

Other lakes have been reported as having two races or sizes of smelts. Whether these represent Osmerus mordax and O. spectrum or two age classes remains to be seen. But these lakes deserve priority in investigating the range of the pygmy smelt. Delisle and Veilleux (1969) report two populations, dwarf and giant, in Lake Champlain (Québec, Vermont and New York), and Lake Kénogami, Québec (Jonquière-Chicoutimi County). They further report allopatric dwarf populations in Lac Grobois (= Batiscan, Laviolette County), Lac Perchaude (St-Maurice County), and Lac Clay and Lac Cole (both in Papineau County), all these lakes being in Québec.

According to Kendall (1927), the following lakes in Maine support sympatric populations of large-sized and small-sized smelts: Sebago Lake (Cumberland County), Cochnewagn Pond (Kennebec County), and Grand Lake (Washington County, also in York County, New Brunswick). He also gave several reports of allopatric occurrences of small-sized smelt. Aside from the Lake Kénogami record, Québec, most of these potential records are within the range circumscribed by verified records of the pygmy smelt.

Until the pygmy smelt is proven to be widespread in its distribution, its native occurrence in only two lakes in Canada, lakes Heney and Utopia, strongly suggests that these

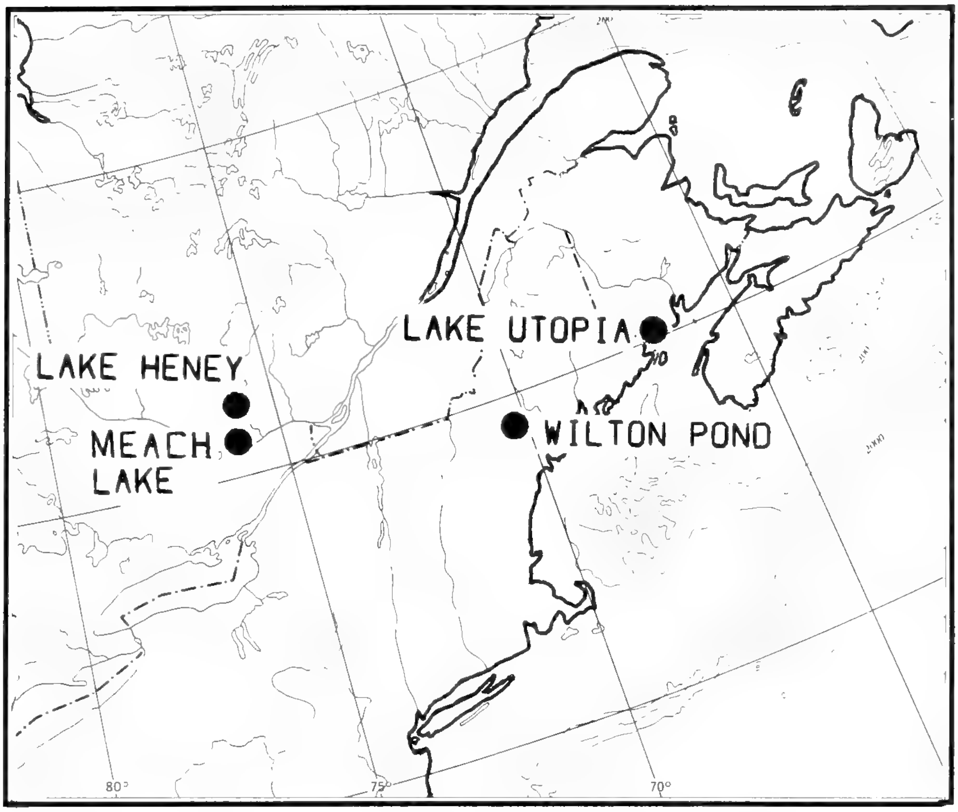

Fig. 6. Geographic distribution of the pygmy smelt, Osmerus spectrum Cope, 1870. The population in Meach Lake, Québec originated from an introduction from Utopia Lake, New Brunswick in 1924.

populations be protected from pollution including acid precipitation, habitat deterioration, overfishing, and introduction of competitors. It deserves protection because of its rarity in its own right as a species and because of its value as a forage fish for sport and commercial fishes for introduction into certain other lakes. A survey of specimens is under way by Sylvie Laframboise and the second author to determine if the pygmy smelt occurs in other lakes.

ORIGIN OF PYGMY SMELT

We find it interesting to speculate on the origin of the pygmy smelt. Given the widespread occurrence of anadromous populations of the rainbow smelt in the Atlantic, Pacific and Arctic waters, it seems most likely to us that *Osmerus spectrum* with its restricted lacustrine range, arose from *Osmerus mordax*. The close morphological and biochemical homogeneity (Copeman, 1977 and unpublished studies by Larry Speirs) of the two species, does not call for an origin earlier than the Pleistocene or perhaps even the Wisconsin.

We hypothesize that *Osmerus spectrum* arose in lakes close to the edge of a Wisconsin or an earlier ice sheet, perhaps during a glacial maximum, on the Atlantic seaboard. Or it might have evolved in one of the proglacial lakes during the Wisconsin glacial retreat, e.g. Glacial Lake Hitchcock in the valley of the Connecticut River which may have endured 4,100 years starting not long before 13,000 BP (Schafer and Hartshorn, 1965). However we personally feel that the level of differentiation, greater than that of the Newfoundland dwarf, suggests an age greater than 15,000 years and an orgin going back to about the mid or early Wisconsin.

Allopatric isolation in a plankton-rich but fish-depauperate lake in the presence of a vacant niche would have favoured retention of the planktivorous over-development of the piscivorous habit as an adult. Or conceivably the pygmy smelt might have evolved sympatrically through interruption of the spawning run by a natural disaster such as a glacial clay land-slide, mutation for a later spawning period, or through selection acting on stocks homing to different spawning grounds in the same lake.

Neoteny with sexual maturity at an earlier age and smaller size while still planktivorous, may have occurred. Selection for more gill rakers in association with prolonged planktivory, and fewer scales and vertebrae because of smaller maximum size in accordance with Lindsey's pleomeristic rule (Lindsey, 1975) may have occurred in initial or secondary sympatry.

Dispersal may have occurred northwards in proglacial lakes or in drainages fed by melting glaciers through New England to southern New Brunswick, with southern populations being extirpated as lakes warmed. Deglaciation of lake basins known to presently contain pygmy smelt in Maine and New Brunswick took place between 13,000 and 14,000 BP (Geological Survey of Canada Map 1257A. Retreat of Wisconsin and Recent ice in North America).

Populations in southern Québec can be no older than deglaciation estimated (Map 1257A. *op. cit.*) at 10,800 to 11,500 BP. The glacial history here is more complicated

(M.J. Dadswell in McAllister and Coad, 1974). First a glacial lake (Lake Belleville-Fort Ann) formed in the Ottawa Valley and neighbouring regions. This was followed by the Champlain Sea, a marine invasion caused by sea levels rising over the land still depressed by the weight of the glaciers. This sea then turned estuarine, lacustrine (Lampsilis Lake) and finally fluvial. We suggest that pygmy smelt, unknown to be anadromous, invaded southern Québec either during the freshwater Lake-Belleville-Fort Ann or the Lampsilis Lake stage. But it cannot be excluded that pygmy smelt retained tolerance to sea water and dispersed along the coast to Maine, New Brunswick, and via the Champlain Sea to the Gatineau Valley. Salinity tolerance tests of pygmy smelt and lacustrine rainbow smelt would be interesting.

When rainbow smelt invaded the Ottawa Valley region is less clear. Fossils probably referable to *Osmerus mordax* dating from approximately 10,000 BP were reported from Green Creek near Ottawa, in the Ottawa Valley by McAllister, Cumbaa and Harington (1981). While the size of the two fossils, about 110 mm SL and 117 mm SL suggests the lacustrine form of the rainbow smelt rather than the anadromous form, it is quite possible that these are subadult anadromous smelts. Whatever the form, the fossils do indicate that smelt had invaded the Ottawa Valley within one or two thousand years of deglaciation.

MANAGEMENT IMPLICATIONS

That there are two species of smelt, one small, one large in eastern North America has several management implications.

If both species occur in the same lake, then separate catch statistics should be kept for each species if the populations are to be regulated. Habitat protection must take into account spawning grounds, spawning times and habitat requirements. Beach and stream spawners are more subject to disturbance, pollution and overfishing than sublittoral lake spawners.

The larger smelt, *Osmerus mordax*, is probably more sought after and subject to capture by the ice fishing angler. But both species would be accessible to capture at spawning time by dip net or seine in populations that spawned after break-up in streams or on beaches.

The interactions of the two smelt species with other species (and between themselves) needs to be considered in managing existing populations or in making introductions. The pygmy smelt is unlikely to feed on the young of other sport fishes or their prey, unlike adult rainbow smelt. Larger pygmy smelt would compete directly with adults of only a few sport and commercial fishes such as ciscos and whitefishes of the genus *Coregonus*. Occurrence of adult pygmy smelt largely in the hypolimnion would preclude their competition with larvae of those sport fishes that are found in the epilimnion. The small size of the pygmy smelt makes them an ideal forage fish for those fishes which share their habitat. Kendall (1927) stated that most lakes naturally inhabited by landlocked salmon were also inhabited by smelt and that there were no instances of successful stocking of any lake with landlocked salmon when smelts were not also introduced. Lake trout, brook trout and other sport fishes also feed on smelts (Kendall, 1927).

The rainbow smelt, because of its larger size, does not lend itself so readily to use as a forage fish, save for larger predators. Indeed its size, dentition and its habits permit it to feed on the young of those sport fishes which co-exist with it. When rainbow smelt are to be introduced for winter angling, one might consider also introducing pygmy smelt as forage for the rainbow smelt to increase their growth.

When smelt introductions are made, it would be wise to take measures to avoid also introducing the microsporidian *Glugea hertwigi* which infects several smelt populations (Legault and Delisle, 1967; Delisle and Veilleux, 1969; Delisle, 1969b, 1972).

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